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**Notes on the Type Specimens
of *Pteranodon* and *Nyctosaurus*
(Pterosauria, Pteranodontidae)
In the Yale Peabody Museum
Collections**

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(Received 8 August 1983)

Abstract

The type specimens of the nine named species of the Cretaceous pterodactyls *Pteranodon* and *Nyctosaurus* housed in the Peabody Museum of Natural History, Yale University, Vertebrate Paleontology Collections are documented and lectotypes for *Pteranodon occidentalis*, *Pteranodon ingens* and *Pteranodon comptus* are herein designated. A thorough revision of *Pteranodon* and *Nyctosaurus* should consider all eighteen named species which have been referred to these genera and should also include specimens currently dispersed throughout numerous museums on several continents. However, preliminary to such a revision, based on the Peabody Museum Collections the following systematic suggestions can be made: 1) *Pteranodon longiceps* and *P. marshi* are junior subjective synonyms of *P. ingens*. 2) *P. comptus* is a junior subjective synonym of *P. velox*. 3) *P. eatoni* is a junior subjective synonym of *P. occidentalis*. 4) "*Nyctosaurus*" *nanus* may be better referred to *Pteranodon*.

Key Words

Pteranodon, *Nyctosaurus*, Cretaceous, Niobrara Formation, Kansas, pterodactyl, flying reptile.

Introduction

In a series of short papers Othniel Charles Marsh (1871, 1872a, 1872b, 1876a, 1876b, 1881, 1884) of the Peabody Museum of Natural History (YPM) at Yale University described the first pterosaurs (pterodactyls) known from North America. His descriptions of two new genera and seven new species (Table 1) of pterosaurs were based on specimens that he and his assistants and field collectors discovered in the upper Cretaceous Niobrara Formation of western Kansas. At the time when Marsh's descriptions of the Kansas pterosaurs were written the present cataloguing system had not yet been instituted for the Vertebrate Paleontology Collections in the Peabody Museum and Marsh did not refer to any of his specimens by number or by any other unambiguous means of identification. Except for Marsh's 1884 paper which included a composite reconstruction of the skull of *Pteranodon longiceps*, all of his papers were unillustrated. Moreover, when describing the specimens on which he based his new genera and species, several times Marsh evidently misidentified various elements of the skeletons, as is discussed below. Marsh planned to write a fuller treatment, presumably an illustrated

Table 1

Named pterosaur species that have been referred to *Pteranodon* and *Nyctosaurus* (listed in order of description).

<i>Pterodactylus occidentalis</i> Marsh, 1872a (= <i>Pterodactylus oweni</i> Marsh, 1871)
<i>Pterodactylus ingens</i> Marsh, 1872a
<i>Pterodactylus velox</i> Marsh, 1872a
" <i>Ornithochirus</i> " <i>umbrosus</i> Cope, 1872
" <i>Ornithochirus</i> " <i>harpyia</i> Cope, 1872
<i>Pteranodon longiceps</i> Marsh, 1876a
<i>Pteranodon gracilis</i> Marsh, 1876a
<i>Pteranodon comptus</i> Marsh, 1876a
<i>Pteranodon nanus</i> Marsh, 1881
<i>Nyctosaurus leptodactylus</i> Williston, 1903
" <i>Ornithostoma</i> " <i>orientalis</i> Bogolubov, 1914
? <i>Pteranodon oregonensis</i> Gilmore, 1928
<i>Nyctosaurus lamegoi</i> Price, 1953
<i>Pteranodon sternbergi</i> Harksen, 1966
<i>Pteranodon</i> (<i>Longicepia</i>) <i>marshi</i> Miller, 1972a
<i>Pteranodon</i> (<i>Nyctosaurus</i>) <i>bonneri</i> Miller, 1972a
<i>Pteranodon</i> (<i>Sternbergia</i>) <i>walkeri</i> Miller, 1972a
<i>Pteranodon</i> (<i>Occidentalia</i>) <i>eatoni</i> Miller, 1972a

monograph, on the North American pterosaurs (as indicated in Marsh 1884), but this was never done.

In the literature following Marsh's pioneering work on pterosaurs there has been much confusion as to which of Marsh's genera and species are valid, in part because the names were not adequately tied to described or illustrated specimens. Thus Williston (1892, p. 6; 1893; 1897; 1903) referred specimens of Kansas pterosaurs to Marsh's genera and species based partly on Marsh's meager descriptions, but also partly on his own recollections of the Yale specimens which he had helped to collect (Schuchert and LeVene 1940). In 1910 Eaton published a monographic study of the osteology of *Pteranodon* based on Marsh's specimens in the Peabody Museum. By this time the present cataloguing system was in use and Eaton (1910) designated by number the specimens he described and illustrated in thirty-one plates, most of which are actual

photographs. Eaton did much to clarify the osteology of *Pteranodon*; however, he did not attempt a systematic revision of the genus, but rather referred to the majority of specimens as "*Pteranodon* sp." Eaton (1910) did state which specimens he believed to be the "types" of several species of *Pteranodon*; but as discussed below, in several instances the specimens which Eaton (1910) designated as types were not even collected until several years after Marsh had named the species. Thus Eaton was clearly mistaken as to the identity of the type specimens. In other cases Eaton (1910) did not even state what specimen might be the type for a given species. Miller (1972a) attempted a revision of *Pteranodon* and *Nyctosaurus* in which he merely perpetuated the errors of Eaton (1910). He also considered a number of Marsh's species, including the first three named, to be nomina dubia and furthermore proposed two new species based on Marsh's specimens without adequate justification. In the most recent review of *Pteranodon* and *Nyctosaurus* Wellnhofer (1978) further perpetuated the errors of Eaton (1910) and Miller (1972a). On the basis of the literature available, it is impossible to determine with certainty what YPM catalogue numbers the type specimens of Marsh's species of *Pteranodon* and *Nyctosaurus* bear or what elements these specimens consist of. Only one of the types, that of *Pteranodon longiceps* Marsh, 1876a, has been illustrated (Eaton 1910, pl. I, fig. 1; pl. V, figs. 1, 7, 8; pl. VI, fig. 11; Miller 1972a, pl. 1, fig. B). In this paper I document the type specimens of *Pteranodon* and *Nyctosaurus* housed in the Yale Peabody Museum and illustrate those that have not been previously illustrated. Finally, I present some brief comments on the present status of the systematics of *Pteranodon* and *Nyctosaurus*.

In the older literature there has been much discussion of whether the wing-finger of pterosaurs is homologous to the fourth or the fifth digit of other tetrapods (see summary of this dispute in Williston 1911). In the older literature on *Pteranodon* and *Nyctosaurus* (see especially Williston 1903, Eaton 1910) the wing-finger is regarded as the fifth digit.

Williston subsequently (1904, 1911) presented a strong case for the homology of the wing-finger with the fourth digit. Here I consider the wing-finger of *Pteranodon* and *Nyctosaurus* to be homologous to digit four, as have most recent workers (Miller 1972b, Mateer 1975, Wellnhofer 1978).

Systematic Paleontology

CLASS Reptilia
ORDER Pterosauria
SUBORDER Pterodactyloidea
FAMILY Pteranodontidae

Included Genera

Pteranodon Marsh, 1876a, *Nyctosaurus* Marsh, 1876b, and *Ornithostoma* Seeley, 1871.

Discussion

Pteranodon, *Nyctosaurus* and *Ornithostoma* are sometimes included with the European *Ornithocheirus* Seeley, 1869 in the *Ornithocheiridae* Seeley, 1870 (Miller 1972a). I here follow Wellnhofer (1978) in considering the *Pteranodontidae* Marsh, 1876a, a distinct family. Also, I here accept the current consensus view that pterosaurs are reptiles although it has been argued, both in this century and the last, that pterosaurs are allied with birds (Seeley 1866, Gardiner 1982).

The Type Specimens of *Pteranodon* and *Nyctosaurus* in the Yale Peabody Museum

Pteranodon occidentalis (Marsh, 1872a)
(Fig. 1)

Synonymy

Pterodactylus oweni Marsh, 1871, p. 472
(preoccupied by *Pterodactylus oweni*
Seeley [see Seeley 1870, p. 115–16]).

Pterodactylus occidentalis Marsh, 1872a,
p. 241.

Pteranodon occidentalis: Marsh, 1876a, p. 508.

Lectotype

YPM 1160, distal end of right metacarpal IV
(Fig. 1A, B).

Horizon and Locality of the Lectotype

Collected by O. C. Marsh from gray shale of the Niobrara Formation, upper Cretaceous, north side or North Fork of the Smoky (Hill) River, probably five miles (=8.05 km) west of Russell Springs, Kansas, in November 1870; possibly on 30 November 1870.

Paralectotypes

YPM 1160, proximal end of ?metacarpal IV (Fig. 1C, D) and phalangeal bone fragments (Fig. 1E, F): locality information same as that for the lectotype.

YPM 1161, distal end of right metacarpal IV: collected by O. C. Marsh from gray shale of the Niobrara Formation, upper Cretaceous, North Fork of the Smoky (Hill) River, east side, one mile (=1.61 km) from the mouth, Kansas, November 1870.

Discussion

Marsh based his new species, *Pterodactylus oweni*, on remains which "belonged to two or more individuals" (Marsh 1871) collected in Kansas the previous fall (i.e., in 1870). According to accession and catalogue records of the Division of Vertebrate Paleontology, Peabody Museum, YPM 1160 and YPM 1161 are the only surviving pterosaur specimens from the 1870 Yale Scientific Expedition and are also the specimens referred to by Marsh (1871). Of these specimens, the best preserved and most diagnostic is the distal end of a right metacarpal IV (Fig. 1A, B). This specimen would appear to be the specimen Marsh (1871) described in the most detail. Marsh (1871) stated that "the length of the shaft



A



B



C



E



F



D

with part of the metacarpal preserved is six and one-half inches [=165 mm]; the fore and aft extent of the condyles fourteen lines [=30.0 mm] and the transverse extent about thirteen lines [=27.5 mm]." The preserved portion of the distal end of metacarpal IV of YPM 1160 is only 65 mm long; however, the largest portion of wing-bone fragment catalogued under YPM 1160 is 98 mm long. Marsh (1871) may have believed that this portion of bone was associated with the distal end of the metacarpal and so arrived at the figure of six and a half inches. It is also possible that the distal end of this metacarpal preserved more of the shaft (now lost) when Marsh (1871) initially studied the specimen. The condyles of this metacarpal measure 30.0 mm long perpendicular to the length of the shaft and 26.0 mm parallel to the length of the shaft; these measurements agree well with Marsh's (1871) "fore and aft extent" and "transverse extent" of the specimen he studied.

There is some evidence, in the form of a nineteenth-century handwritten note associated with YPM 1160, that the fragments catalogued under this number may have been collected on two different occasions by O. C. Marsh, on an unspecified day in November 1870 and on 30 November 1870. Consequently, it is not certain that all of the fragments catalogued under YPM 1160 pertain to a single individual. Therefore, I here designate the distal end of the right metacarpal IV, YPM 1160 (Fig. 1A, B), the lectotype of *Pteranodon occidentalis* (Marsh, 1872a). The remaining fragments catalogued under YPM 1160, and YPM 1161, which Marsh (1871) evidently referred to when describing

P. occidentalis are here considered paralectotypes of the species.

In his original description of pterosaurs from the Cretaceous of Kansas, Marsh (1871) stated that these animals had "smooth and compressed" teeth. Subsequently Marsh (1876a) realized that these forms lacked teeth (the basic character for his new suborder Pteranodontia) and the teeth, which were presumably fish teeth, were removed from the early collections of Kansas pterosaurs.

Eaton (1910, p. 1) stated "that of the three individual specimens [not listed by Eaton] originally referred to *Pteranodon occidentalis*, only one, No. 1164, is complete enough to be of any value. . . ." Accordingly, Eaton (1910, p. 38) designated YPM 1164 a type of *Pteranodon occidentalis*. Eaton (1910, p. 1) also stated that "Professor Marsh observed the form of the jaws of *P. occidentalis* in a fragmentary skull, No. 1179, and from his notes it is evident that he considered this specimen also a type of the species." Thus Eaton (1910, p. 38) designated YPM 1179 the "type skull" of *P. occidentalis*.

According to the Division of Vertebrate Paleontology accession and catalogue records, and also according to Eaton (1910, p. 38), YPM 1164 was collected by O. C. Marsh from gray-blue shale of the Niobrara Formation, upper Cretaceous, north side of the Smoky (Hill) River, western Kansas, July 1871. Thus, this specimen was not collected until after the publication (in June 1871) of the initial description of *Pterodactylus occidentalis* (initially described under the preoccupied name *Pterodactylus oweni* Marsh, 1871) and cannot be part of the type series. YPM 1164 consists of the majority of the bones of the right wing of a single individual (Eaton 1910, pl. XIX, figs. 9–19); this was the most complete specimen of a pterosaur collected by the Yale Scientific Expedition of 1871 and is evidently the specimen which Marsh (1872a, p. 242–45) described at length and referred to *Pterodactylus occidentalis*.

Also, according to museum records and Eaton (1910, p. 38), YPM 1179, a fragmentary skull (Eaton 1910, pl. III, fig. 2), was collected by E. W. Guild (alias E. S. Field) from yellow

◀ Fig. 1

YPM 1160, the lectotype (A, B) and two paralectotypes (C–F) of *Pteranodon occidentalis*: A, distal end of right metacarpal IV, anterolateral view; B, distal end of right metacarpal IV, posterolateral view; C, D, two views of proximal end of ?metacarpal IV; E, F, two views of undetermined wing-bone fragment. Scale = 3 cm.

chalk of the Niobrara Formation, upper Cretaceous, along the Smoky (Hill) River near Castle Rock, Trego County, Kansas, in 1875. As this specimen was collected four years after the initial description of *Pterodactylus occidentalis*, it cannot be part of the type series.

Miller (1972a) accepted YPM 1164 as the type specimen of *Pteranodon occidentalis*, but considered this name to be a nomen dubium and designated YPM 1179 the holotype and only known specimen of a new species, *Pteranodon eatoni*. Wellnhofer (1978,

p. 62–63) listed both *P. occidentalis* and *P. eatoni* as valid and gave their types as YPM 1164 and YPM 1179 respectively.

***Pteranodon ingens* (Marsh, 1872a)**

(Figs. 2, 3)

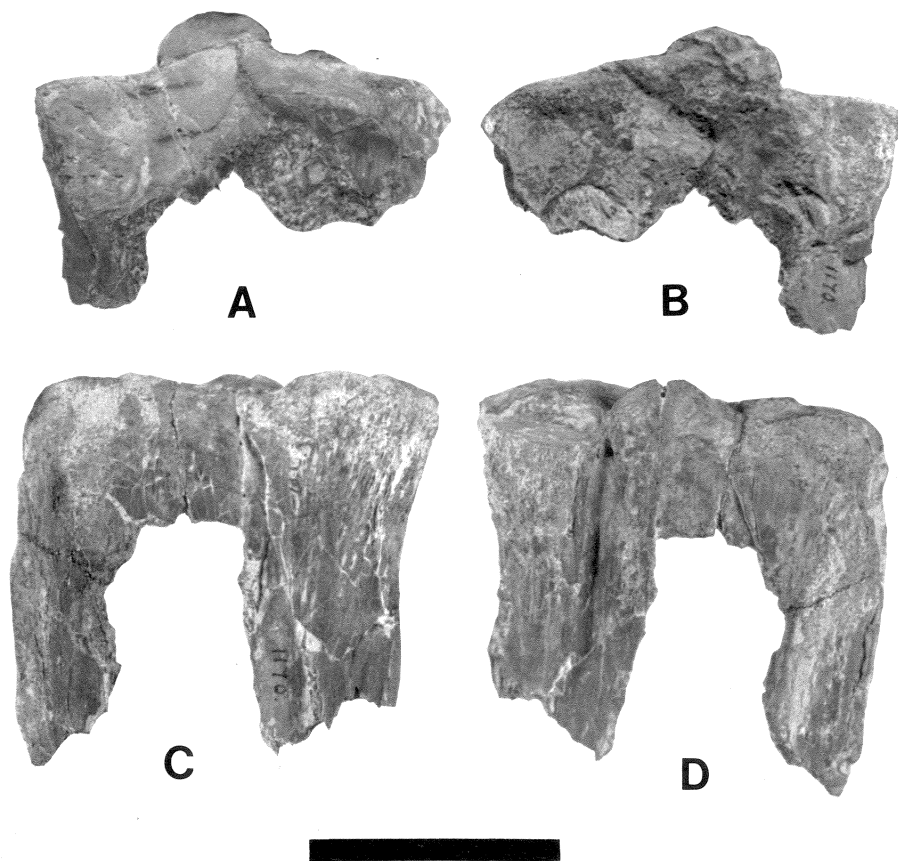
Synonymy

Pterodactylus ingens Marsh, 1872a, p. 246.

Pteranodon ingens: Marsh, 1876a, p. 508.

Fig. 2

YPM 1170, lectotype of *Pteranodon ingens*: A, B, two views of proximal end of ?ulna; C, D, two views of proximal end of ?metacarpal IV. Scale = 4 cm.



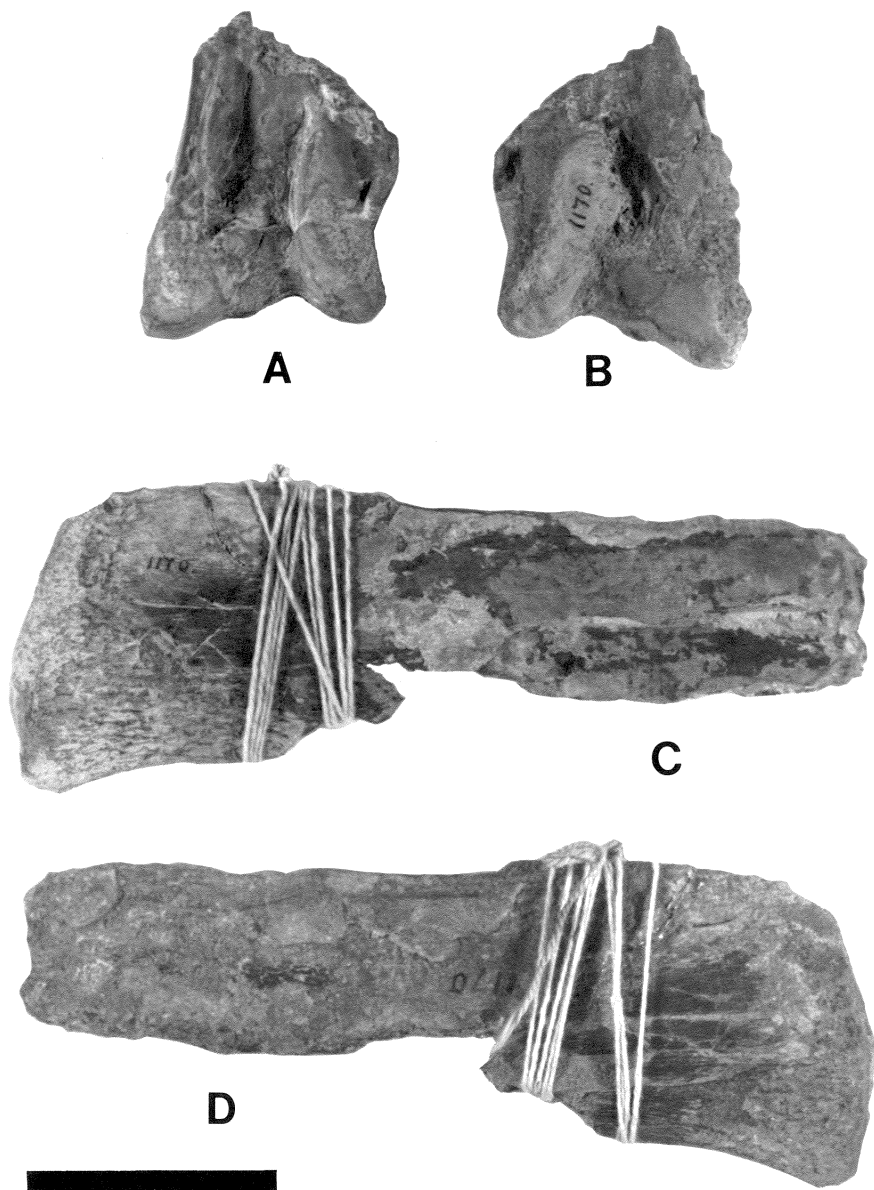


Fig. 3
YPM 1170, lectotype of *Pteranodon ingens*: *A*,
anterior view of distal end of right metacarpal IV; *B*,
posterior view of distal end of right metacarpal IV;
C, *D*, two lateral views of distal end of first phalanx
of digit IV. Scale = 4 cm.

Lectotype

YPM 1170, distal end of right metacarpal IV (Fig. 3A, B), proximal end of ?metacarpal IV (Fig. 2C, D), proximal end of ?ulna (Fig. 2A, B), distal end of first phalanx of digit IV (Fig. 3C, D), and other wing-bone fragments.

Horizon and Locality of the Lectotype

Collected by O. C. Marsh from gray shale of the Niobrara Formation, upper Cretaceous, probably from the north side of the Smoky (Hill) River, eighteen miles (=30.0 km) east of Fort Wallace, Kansas, July 1871. There is a slight discrepancy between locality information on a nineteenth-century handwritten note with YPM 1170 and locality information for this specimen in the Division of Vertebrate Paleontology old catalogue of Cretaceous fossils. The handwritten note with YPM 1170 contains the locality information which, according to the old catalogue, belongs with YPM 1171 (see below); this note may have been misplaced in the wrong box.

Paralectotypes

YPM 1169, proximal end of ?first phalanx of digit IV and numerous wing-bone fragments (also catalogued under YPM 1169 are two shark's teeth): collected by O. C. Marsh from gray shale of the Niobrara Formation, upper Cretaceous, south side of the Smoky (Hill) River, twenty miles (=32.2 km) east of Fort Wallace, Kansas, 27 July 1871.

YPM 1171, distal end of left metacarpal IV and bone fragment: collected by O. C. Marsh from gray shale of the Niobrara Formation, upper Cretaceous, south side of the Smoky Hill River, twenty miles (=32.2 km) east of Fort Wallace, Kansas, 26 July 1871.

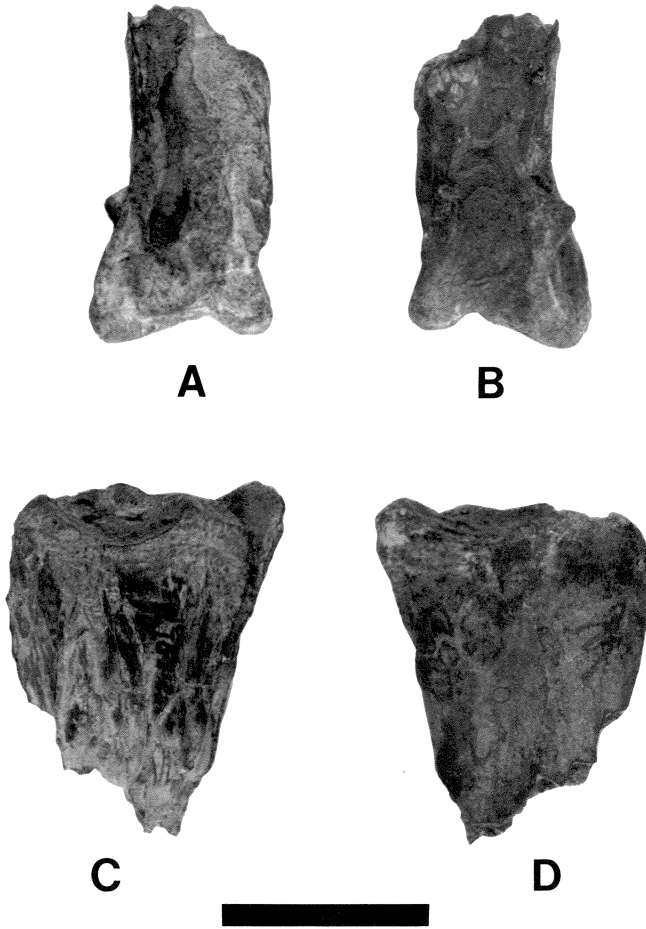
YPM 1172, distal end of right metacarpal IV and two bone fragments: collected by O. Harger from yellow shale of the Niobrara Formation, upper Cretaceous, north side of the Smoky (Hill) River, twenty-six (=41.9 km) miles east of Fort Wallace, Kansas, 31 July 1871.

Discussion

Marsh (1872a, p. 246) based his species *Pterodactylus ingens* on "specimens pertaining to four individuals," collected during the summer of 1871, of a pterosaur larger than *Pterodactylus occidentalis*. According to the Division of Vertebrate Paleontology accession and catalogue records, these four individuals are YPM 1169, YPM 1170, YPM 1171 and YPM 1172; these specimens also match the description given of them by Marsh (1872a, p. 246–47). As YPM 1170 is the most complete specimen, I here designate it the lectotype of *Pteranodon ingens* (Marsh, 1872a). The remaining specimens can be considered paralectotypes of this species.

In regard to *Pteranodon ingens*, Eaton (1910, p. 1) stated that "one of the types, No. 1175, is a magnificent but incomplete skeleton, which does not include the fifth [i.e., fourth] digit of the hand, the so-called wing finger. Another valuable type of this species is the large nearly complete skull, No. 2594. . . ." According to the Division of Vertebrate Paleontology accession and catalogue records, and also according to Eaton (1910, p. 38), both YPM 1175 and YPM 2594 were collected after Marsh's initial description of *P. ingens* and therefore cannot be types of the species. YPM 1175 (thoroughly described and illustrated by Eaton 1910, pl. VI, figs. 1–6, 12–15; pl. X, fig. 1; pl. XI, figs. 1–3; pl. XVI, fig. 4; pl. XVII, fig. 1; pl. XIX, figs. 1–8; pl. XXVII, figs. 4, 5) was collected by E. S. Field (alias E. W. Guild) of B. F. Mudge's party from yellow chalk of the Niobrara Formation, upper Cretaceous, near the Smoky (Hill) River, Wallace County, Kansas, 17 May 1876. YPM 2594 (Eaton 1910, pl. II, fig. 1; pl. III, fig. 1) was collected by S. W. Williston from yellow chalk of the Niobrara Formation, upper Cretaceous, near the Smoky (Hill) River, Wallace County, Kansas, 20 July 1877.

Miller (1972a) accepted YPM 1175 as the type specimen of *Pteranodon ingens*, but considered this name to be a nomen dubium. Without documentation, Miller (1972a, p. 7) states that the bones catalogued as YPM 1175 came from at least two different

**Fig. 4**

YPM 1176, holotype of *Pteranodon velox*:

A, anterior view of distal end of right metacarpal IV;
B, posterior view of distal end of right metacarpal IV;
C, D, two lateral views of proximal end of right first phalanx of digit IV. Scale = 3 cm.

localities. However, I have found no evidence to support Miller's statement. Miller (1972a, p. 9–10) designated YPM 2594 the holotype and only referred specimen of a new species of *Pteranodon*, *P. marshi*. Wellnhofer (1978) perpetuated the error of considering

YPM 1175 to be the type of *P. ingens* and also listed *P. marshi* as presumably valid.

***Pteranodon velox* (Marsh, 1872a)**
(Fig. 4)

**Fig. 5**

YPM 1178, holotype of *Nyctosaurus gracilis*: pectoral region seen in posterior view, lateral view of cervical vertebrae and ventral view of dorsal vertebrae; see Fig. 6 for explanation. Scale = 3 cm.

Synonymy

Pterodactylus velox Marsh, 1872a, p. 247.
Pteranodon velox: Marsh, 1876a, p. 508.

Holotype

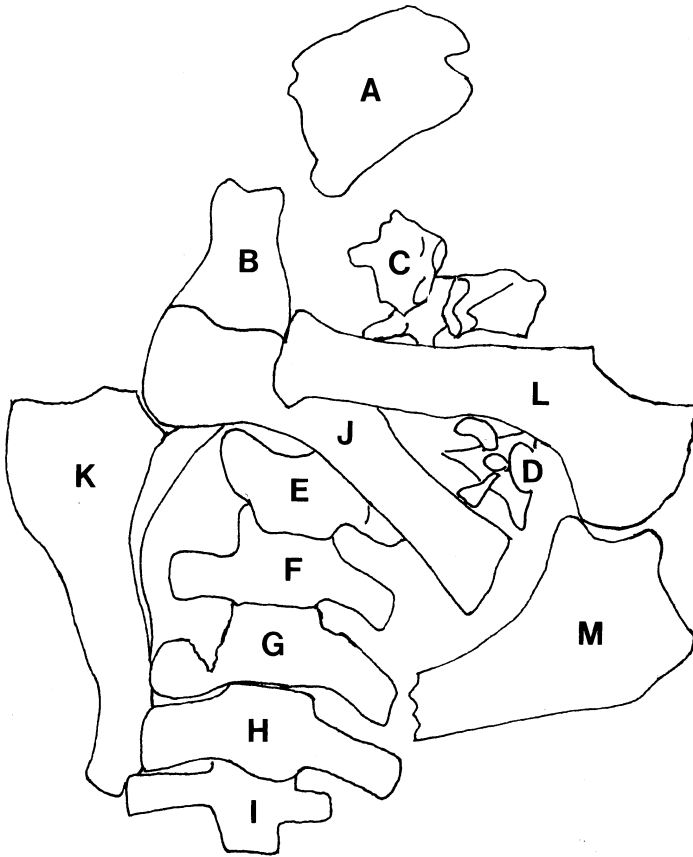
YPM 1176, distal end of right metacarpal IV (Fig. 4A, B) and proximal end of right first phalanx of digit IV (Fig. 4C, D).

Horizon and Locality of the Holotype

Collected by O. C. Marsh from gray-blue shale of the Niobrara Formation, upper Cretaceous, south side of the Smoky (Hill) River, twenty-six (=41.9 km) miles east of Fort Wallace, Kansas, 27 July 1871.

Paratypes

None.

**Fig. 6**

YPM 1178, holotype of *Nyctosaurus gracilis* (compare to Fig. 5): A, B, cervical vertebrae in lateral view; C, dorsoventrally crushed vertebra; D, posterior view of ?cervical vertebra; E-I, ventral view of five free dorsal vertebrae; J, posterior view of right coracoid; K, posterior view of right scapula; L, posterior view of left coracoid; M, posterior view of left scapula.

Discussion

Accession and catalogue records of the Division of Vertebrate Paleontology are in agreement that YPM 1176 is the sole specimen upon which Marsh (1872a) based his description of *Pterodactylus velox*. Moreover, YPM 1176 agrees perfectly with the description and measurements given by

Marsh (1872a, p. 247-48). Eaton (1910) did not state the number of the type specimen of *Pteranodon velox*. However, Miller (1972a), who considered the specific name a nomen dubium, listed the type as YPM 1176. Wellnhofer (1978) did not discuss *Pteranodon velox*, but merely included it in a list of "Pteranodontidae incertae sedis."



Fig. 7

YPM 1178, holotype of *Nyctosaurus gracilis*: pectoral region seen in anterior view; lateral view of cervical vertebrae and dorsal view of dorsal vertebrae; compare to Figs. 5 and 6. Scale = 3 cm.

***Pteranodon longiceps* Marsh, 1876a**

Synonymy

Pteranodon longiceps Marsh, 1876a, p. 508.

Holotype

YPM 1177, nearly complete skull (Eaton 1910, pl. I, fig. 1; pl. IV, figs. 1, 7, 8; Miller 1972a, pl. 1, fig. B), atlas and axis (Eaton 1910, pl. VI, fig. 11).

Horizon and Locality of the Holotype

Collected by S. W. Williston from yellow chalk of the Niobrara Formation, upper Cretaceous, near the Smoky (Hill) River, Wallace County, Kansas, 2 May 1876.

Paratypes

None.

**Fig. 8**

YPM 1178, holotype of *Nyctosaurus gracilis*: A, right first phalanx of digit IV; B, right carpals and metacarpal IV; C, left first phalanx of digit IV; D, left ulna, radius, carpals and metacarpal IV.

Scale = 10 cm.

Discussion

Pteranodon longiceps was the fourth species of pterosaur described by Marsh from the upper Cretaceous strata of Kansas and is the type species of the genus *Pteranodon*. According to the Division of Vertebrate Paleontology accession records, YPM 1177 was shipped from Buffalo Station, Kansas, and received at Yale on 13 May 1876. The skull was unpacked, Marsh wrote his brief description of the specimen, submitted it to the *American Journal of Science* on 15 May 1876 and it was published in June of that year. All sources and subsequent authors unanimously agree that YPM 1177 is the type of *Pteranodon longiceps*.

***Nyctosaurus gracilis* (Marsh, 1876a)** (Figs. 5–8)

Synonymy

Pteranodon gracilis Marsh, 1876a, p. 508.
Nyctosaurus gracilis: Marsh, 1876b, p. 480.
Nyctodactylus gracilis: Marsh, 1881, p. 343.

Holotype

YPM 1178, right and left scapulae and coracoids, two cervical vertebrae, five free dorsal vertebrae, another ?dorsal vertebra, ?eighth cervical vertebra (Figs. 5–7: see Williston 1903, p. 133), left ulna and radius, right and left carpals, right and left fourth metacarpals, right and left first phalanges of the fourth digit (Fig. 8).

Horizon and Locality of the Holotype

Collected by H. A. Brous from strata of the Niobrara Formation, upper Cretaceous, Huckberry, Gove County, Kansas, 21 April 1876.

Paratypes

None.

Discussion

All records and authorities agree that YPM 1178 is the type specimen of *Nyctosaurus gracilis*. This specimen matches Marsh's (1876a, p. 508) original description of it, except that initially Marsh mistook the shoulder girdle for a "nearly complete pelvis." Marsh however realized his mistake and published a brief, corrected description of this specimen (Marsh 1876b, p. 480) without, however, clearly stating his original error. As a consequence, Williston (1892, p. 6) believed that Marsh had described two different specimens in these two papers: one which included a pelvis (Marsh 1876a) and another which included a scapula and coracoid (Marsh 1876b).

Nyctosaurus gracilis was initially described as a species of *Pteranodon* (Marsh 1876a); but shortly thereafter Marsh (1876b) made it the type species of the genus *Nyctosaurus*.

***Pteranodon comptus* Marsh, 1876a** (Fig. 9)

Synonymy

Pteranodon comptus Marsh, 1876a, p. 509.

Lectotype

YPM 2335, distal ends of right and left tibiae and ?right tarsals (Fig. 9).

Horizon and Locality of the Lectotype

Collected by B. F. Mudge from strata of the Niobrara Formation, upper Cretaceous, "Town and Range 23," Graham County, Kansas, 17 May 1875.

Specimens Previously Considered Cotypes of the Species But Not Considered Paralectotypes Here

YPM 2287, centra of two dorsal vertebrae and many fragments of bone and fish teeth:

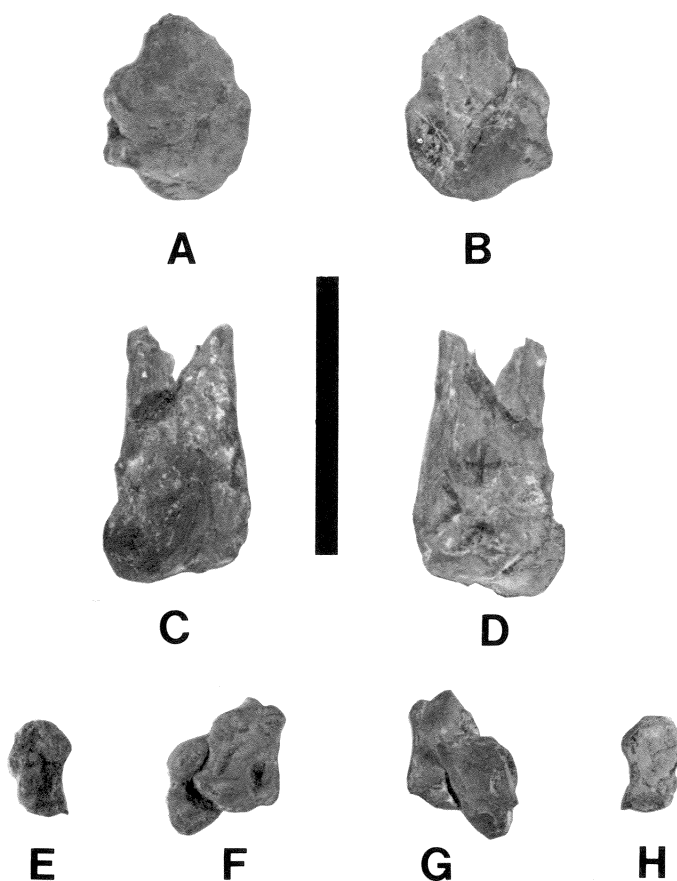


Fig. 9
YPM 2335, the lectotype of *Pteranodon comptus*: *A*, anterior view of distal end of left tibia; *B*, posterior view of distal end of left tibia; *C*, anterior view of distal end of right tibia; *D*, posterior view of distal end of right tibia; *E*, *F*, proximal view of three right tarsals; *G*, *H*, distal view of three right tarsals. The tarsals as figured positioned in *E* and *F* have been rotated 180 degrees around their vertical axes (relative to the page) to their positions as figured in *G* and *H*. Scale = 3 cm.

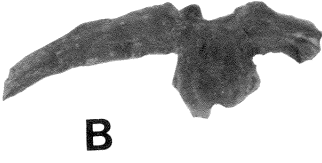
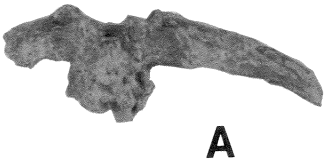
collected by O. C. Marsh from strata of the Niobrara Formation, upper Cretaceous, western Kansas, 21 October 1872.

YPM 2397, distal end of ?femur, distal end of tibia and fragmentary metatarsals: collected by E. S. Field from strata of the Niobrara

Formation, upper Cretaceous, Wallace County, Kansas, 29 April 1876.

Discussion

Marsh (1876a, p. 509) described *Pteranodon*



comptus on the basis of "three skeletons" which included "two distal ends of the characteristic metacarpal of the wing finger, other portions of the wing bones, and two sacral vertebrae." Division of Vertebrate Paleontology accession and catalogue records indicate that YPM 2335 and YPM 2287 are the "types" of *P. comptus* "in part." As Eaton (1910, p. 2-3) pointed out, the distal ends of the tibiae of YPM 2335 fit exactly the description and measurements of the supposed wing metacarpals of *P. comptus* described by Marsh (1876a). The crushed distal end of the tibia looks very much like the distal end of the metacarpal IV and I agree with Eaton (1910) that Marsh probably confused these two bones. Therefore, I here designate YPM 2335 the lectotype of *Pteranodon comptus*.

As Eaton (1910, p. 2-3) also noted, the two centra of dorsal vertebrae which are catalogued under YPM 2287 fit the description and measurements given by Marsh (1876a) of the supposed sacral vertebrae of *Pteranodon comptus*. Thus, Marsh may have based his description of this species partly on this specimen. However, at present there is no way unequivocally to associate YPM 2287 with the same species as is represented by YPM 2335. Eaton (1910, p. 3) stated, without justification, that "associated with these types [YPM 2335 and YPM 2287] in the collection is No. 2397. . . ." Division of Vertebrate Paleontology records, however, do not give any indication that this specimen was ever considered a possible type of *P. comptus* prior to Eaton's (1910) monograph. Moreover, as Eaton (1910) states, YPM 2397 may consist of parts of two individuals.

Miller (1972a) considered *Pteranodon comptus* to be a nomen dubium and did not list a type specimen for it. Wellnhofer (1978) merely listed the name *Pteranodon comptus* under "Pteranodontidae incertae sedis."

***Nyctosaurus nanus* (Marsh, 1881)**

(Fig. 10)

Synonymy

Pteranodon nanus Marsh, 1881, p. 343.
(?)*Pteranodon nanus*: Williston, 1903, p. 157.
"*P. nanus* . . . referred to *Nyctosaurus*":
Eaton, 1910, p. 3.

Holotype

YPM 1182, left scapula (Fig. 10C, D), left coracoid (Fig. 10C, D), left humerus (Fig. 10E, F), trunk vertebra with ankylosed rib (Fig. 10A, B), and other bone fragments.

Horizon and Locality of the Holotype

Collected by S. W. Williston from strata of the Niobrara Formation, upper Cretaceous, on the line between Graham and Rooks Counties, Kansas, 22 September 1876.

Paratypes

None.

Discussion

All records and authorities agree that YPM 1182 is the type specimen of *Pteranodon nanus* and Marsh's (1881) brief description and measurements match YPM 1182 perfectly.

Williston (1903, p. 157) suggested that *Pteranodon nanus* may be a synonym of *Nyctosaurus gracilis*, and Eaton (1910) stated that *P. nanus* should be referred to *Nyctosaurus*. Miller (1972a, p. 12) wrote that *P. nanus* "may either belong to that species [*Nyctosaurus gracilis*] or be a smaller and valid, although as yet poorly known, species."

◀ Fig. 10

YPM 1182, holotype of *Nyctosaurus nanus*:
A, dorsal view of trunk vertebra with ankylosed rib;
B, ventral view of trunk vertebra with ankylosed rib;
C, anterior view of left scapula and coracoid;
D, posterior view of left scapula and coracoid;
E, external view of left humerus; F, internal view of left humerus. Scale = 3 cm.

Wellnhofer (1978, p. 64) synonymized *Pteranodon nanus* with *Nyctosaurus gracilis*. (For further discussion of this species, see below, p. 19.)

***Pteranodon marshi* Miller, 1972a**

Synonymy

Pteranodon marshi Miller, 1972a, p. 9.

Discussion

As noted above (p. 9), Miller (1972a) designated YPM 2594 the holotype and only known specimen of *Pteranodon marshi*.

***Pteranodon eatoni* Miller, 1972a**

Synonymy

Pteranodon eatoni Miller, 1972a, p. 9.

Discussion

As noted above (p. 6), Miller (1972a) designated YPM 1179 the holotype and only known specimen of *Pteranodon eatoni*.

Comments on the Genera *Pteranodon* and *Nyctosaurus*

Marsh (1871, 1872a, 1872b) initially referred the pterosaurs from Kansas to the European genus *Pterodactylus*. Cope (1872) also described two species of pterosaurs from the Cretaceous of Kansas, referring them to the European genus *Ornithocheirus* (misspelled as "*Ornithochirus*" by Cope). Marsh (1872b) asserted that Cope's species, *O. umbrosus* and *O. harpyia* are junior subjective synonyms of his own species, *Pterodactylus occidentalis* and *P. ingens* respectively. Cope later (e.g., 1875) accepted Marsh's referral of the Kansas species to *Pterodactylus* and also Marsh's (1872b) synonymy of *O. harpyia* Cope (published 9 March 1872) with *P. occidentalis*

Marsh (published 7 March 1872). Cope, however, retained his species *P. umbrosus* as specifically distinct.

The unanimous consensus of subsequent workers (e.g., Williston 1892, Miller 1972a, Wellnhofer 1978) has been to consider Cope's species as belonging to the same genus as Marsh's two species cited above, although not necessarily accepting Marsh's synonymies at the specific level.

In 1876 Marsh recognized that the Kansas pterosaurs which he had referred to *Pterodactylus* differed from the European genus in lacking teeth and bearing a large, distinctive, posteriorly-directed sagittal crest, among other features. Accordingly, Marsh (1876a) erected the new genus *Pteranodon* for these Kansas forms. Shortly thereafter Marsh (1876b) recognized that the species he had described as *Pteranodon gracilis* Marsh, 1876a, differed from all previously described species of *Pteranodon*, in bearing a distinct coracoid which was not fused with the scapula, and erected the genus *Nyctosaurus* for this species. In 1881 Marsh proposed the replacement name *Nyctodactylus* for this genus in the mistaken belief that the name *Nyctosaurus* was preoccupied (see below).

Williston, the next major student of the Kansas pterosaurs at first (1892) accepted Marsh's genera, *Pteranodon* (composed of the species *P. occidentalis* [= *P. harpyia*], *P. ingens*, *P. umbrosus*, *P. velox*, *P. longiceps*, *P. comptus* and *P. nanus*) and *Nyctodactylus* [= *Nyctosaurus*] (including only *N. gracilis*), as distinct. However, after reading a paper by Seeley (1891), Williston was convinced that Marsh's genus *Pteranodon* is a junior subjective synonym of Seeley's European genus *Ornithostoma* Seeley, 1871. Over the next decade Williston (1893, 1897, 1902b, 1903) variously referred to this genus as "*Ornithostoma (Pteranodon)*," "*Pteranodon (Ornithostoma)*," "*Pteranodon or Ornithostoma*" and "*Pteranodon*." Later, Williston (1911, 1912) appears to have accepted Marsh's *Pteranodon* as a fully valid genus.

In the early twentieth century George F. Eaton of Yale's Peabody Museum began to

study in detail Marsh's collection of Kansas pterosaurs. Eaton (1903, 1904, 1910) thoroughly described the distinct "*Pteranodon*" from Kansas and consistently regarded *Pteranodon* as a valid genus. Most subsequent workers have followed Eaton in regarding *Pteranodon* as distinct (Gilmore 1928; see summaries in Miller 1972a, Wellnhofer 1978).

Much of the confusion between the genera *Ornithostoma* Seeley, 1871, and *Pteranodon* Marsh, 1876a, stems from the poor quality of the material upon which the former genus is based. Owen (1859, pl. IV, figs. 4, 5) described a fragment of bone from the Cambridge Greensand (Cenomanian) as the proximal part of the fourth metacarpal of a pterosaur. Seeley (1871) reinterpreted this fragment as part of the premaxillary of a toothless pterosaur and provisionally dubbed it *Ornithostoma*. Since then very little material has been definitely referred to *Ornithostoma* and the status of this genus and its relationship to *Pteranodon* is currently uncertain (Miller 1972a, Wellnhofer 1978).

In the first decade of this century Williston (1902a, 1902b, 1903) published several detailed studies of the osteology of *Nyctosaurus*. Williston (1903, p. 125) pointed out that Marsh (1881) was mistaken in his belief that the generic name *Nyctosaurus* was preoccupied and thus restored the original name for the genus. Williston (1903, p. 157) suggested that *Pteranodon nanus* might be referable to *Nyctosaurus* and further that it might be a synonym of *N. gracilis*. Apparently, this action by Williston (1903) was based primarily on the small size of *P. nanus*. Williston (1903) and later writers (Eaton 1910, Miller 1972a, Wellnhofer 1978) have all sorted out the smallest Kansas pterosaur specimens as *Nyctosaurus* as opposed to the larger *Pteranodon*. Eaton (1910) and Miller (1972a) both referred *P. nanus* to *Nyctosaurus* and Wellnhofer (1978) accepted Williston's (1903) synonymy of *N. gracilis* with *P. nanus*. However, these workers all appear to have ignored the fact that with regard to *Pteranodon nanus* Marsh (1881, p. 343) stated that "the scapula and coracoid were firmly

ankylosed," a supposed character of *Pteranodon*. One of the supposed diagnostic characters of *Nyctosaurus* is that these two bones are not fused. My recent inspection of the scapula-coracoid of the holotype of *P. nanus* (Fig. 10C, D) reveals that they are indeed fused as in other species of *Pteranodon*. The suture between these two bones passes transversely through the middle of the glenoid articular surface (cf. Williston 1903, p. 140, pl. XLIII, fig. 6 and the holotype of *N. gracilis*; Figs. 5-7 of this paper). However, the coracoid has been broken in the holotype of *P. nanus* just below the glenoid surface. I believe a thorough restudy of all known specimens of *Pteranodon* and *Nyctosaurus* needs to be undertaken to definitively establish the generic identity of *P. nanus*. However, following the usage of the most recent literature, I refer to this species as *Nyctosaurus nanus*.

Following Marsh, Williston and Eaton, the next major student of the Kansas pterosaurs was Miller who last revised the genera *Pteranodon* and *Nyctosaurus* (Miller 1972a). Miller (1972a) regarded *Nyctosaurus* as a subgenus of *Pteranodon* and also proposed three other, new, subgenera of *Pteranodon*: *Longicepia* (type species: *P. longiceps* Marsh, 1876a), *Sternbergia* (type species: *P. sternbergi* Harksen, 1966) and *Occidentalia* (type species: *P. eatoni* Miller, 1972a). Miller (1973) subsequently pointed out that *Pteranodon* (*Longicepia*) is a junior objective synonym of *Pteranodon* (*Pteranodon*) as both are based on the same type species. Miller (1978) proposed the new name *Geosternbergia* for *Sternbergia* Miller, 1972a which is a homonym of both *Sternbergia* Paula Couto, 1970 and *Sternbergia* Jordan, 1925.

Miller's (1972a) subgeneric distinctions were based primarily on supposed features of body size and crest proportions. Each subgenus, however, was based on only one or two specimens and as discussed above and below, there are probably problems with Miller's (1972a) species-level taxonomy upon which the subgenera are based. Miller's (1972a) classification has not been generally

accepted. Wellnhofer (1978) retained *Nyctosaurus* and *Pteranodon* as distinct genera, but synonymized the subgenera *Geosternbergia* and *Occidentalia* with the subgenus *Pteranodon* (*Pteranodon*).

Comments on the Species of *Pteranodon* and *Nyctosaurus*

Eighteen named species have been referred or tentatively referred to the genera *Pteranodon* and *Nyctosaurus* (Table 1). I believe that a complete restudy of all known specimens of the Pteranodontidae needs to be undertaken before these genera and their included species can be thoroughly revised. Unfortunately the relevant specimens are housed in a number of different institutions scattered over several continents (see Wellnhofer 1978) and relatively few specimens have been adequately described and illustrated in the literature. However, based on my study of the YPM collection I will make a few comments on the species whose types are preserved in the Peabody Museum.

The first three named species of *Pteranodon* described by Marsh (1871, 1872a) were separated from one another primarily on the basis of size. In order of increasing size these three species are: *P. velox*, *P. occidentalis* and *P. ingens*. The type specimens of these three species (respectively YPM 1176, Fig. 4; YPM 1160, Fig. 1; YPM 1170, Figs. 2, 3) include the distal ends of metacarpal IV which are thus directly comparable. As Marsh stated, these specimens do differ in size and are readily recognizable; but it is not certain that these recognizable morphs represent distinct, "biological" species. They may merely represent a growth series of a single (or perhaps two) species. Despite the 500 catalogued specimens, there is not enough suitably complete skeletal material in the YPM Kansas pterosaur collections to attempt a meaningful statistical analysis of growth trends in *Pteranodon* which might help resolve this problem (cf. Mateer's 1976 statistical study based on thirty-five specimens of

Pterodactylus). However, as these morphs are recognizable I here provisionally regard them as distinct species.

The fourth species named by Marsh (1876a, p. 508), *Pteranodon longiceps*, is based on a single skull (YPM 1177, Eaton 1910, pl. I, fig. 1) which shares no elements in common with the type specimens of Marsh's three previously named species. Marsh (1876a, p. 508) stated that *P. longiceps* "is somewhat larger than *P. occidentalis*." However, YPM 2473, another Cretaceous pterosaur specimen from Kansas, includes a crest (Eaton 1910, pl. II, fig. 2), the distal end of the metacarpal and the proximal end of the first phalanx of right digit IV, and a number of postcranial skeletal fragments which presumably pertain to a single individual. The crest of YPM 2473 appears to "fit" the type skull of *P. longiceps* (which is missing the supraoccipital crest). The metacarpal and first phalanx of digit IV of YPM 2473 are indistinguishable in size and morphology from the corresponding elements of YPM 1170, the type specimen of *P. ingens*. On this basis I suggest that *P. longiceps* Marsh, 1876a is a junior subjective synonym of *P. ingens* Marsh, 1872a.

As described above (p. 17), Marsh (1876a) based *Pteranodon comptus* primarily on YPM 2335, the distal ends of the tibiae of a Kansas pterosaur. In the mistaken belief that these were the fourth metacarpals, Marsh (1876a, p. 509) diagnosed this species as "the smallest pterodactyle [then] known from American strata." YPM 2738 (illustrated and described in Eaton 1910, pl. XXVIII, figs. 1-4) is a partial skeleton of *Pteranodon* from the Cretaceous strata of Kansas. YPM 2738 is unambiguously referable to *Pteranodon ingens* on the basis of the identity in size and morphology of comparable elements, in particular the first phalanx of digit IV, in YPM 2738 and YPM 1170 (the type specimen of *P. ingens*). YPM 2738 includes the two complete tibiae; these tibiae are approximately one and a half times (in linear dimensions) larger than those of YPM 2335 and thus *P. comptus* may have been approximately two-thirds the size of *P. ingens*.

Likewise, YPM 1176 (Fig. 4), the holotype of *P. velox*, represents a pterosaur that was approximately two-thirds the size of *Pteranodon ingens* based on comparison of the fourth metacarpals in YPM 1176 and YPM 1170 (Fig. 3A, B). Thus the type specimens of *P. comptus* and *P. velox* both appear to represent species of *Pteranodon* that are two-thirds the size of *P. ingens*, but *P. comptus* and *P. velox* are not presently distinguishable from one another. Therefore, I suggest that *P. comptus* Marsh, 1876a is a junior subjective synonym of *P. velox* (Marsh, 1872a).

As noted above (p. 19), *Nyctosaurus gracilis* (Marsh, 1876a) is distinctive in bearing an unfused coracoid-scapula and is also smaller than all other species of Kansas pterosaurs with the exception of *N. nanus* (Marsh, 1881). *N. nanus* is easily recognized by its extremely small size; however, as I suggested above (p. 19) it is not clear that *N. nanus* should necessarily be associated with *N. gracilis* in the genus *Nyctosaurus*.

Miller (1972a), without adequate justification, considered *Pteranodon occidentalis* and *P. ingens* nomina dubia. Miller (1972a) then designated two skulls (both described and illustrated in Eaton 1910) in the Peabody collections, YPM 1179 (a medium-sized skull) and YPM 2594 (a large skull), the types and only known specimens of two new species, *Pteranodon eatoni* and *Pteranodon marshi* respectively. YPM 1179 and YPM 2594 do not include any postcranial elements and thus cannot be directly compared to Marsh's type specimens other than that of *P. longiceps*. Furthermore, Miller (1972a) did not differentiate these supposed species from Marsh's earlier named morphs. Previously, Eaton (1910) considered YPM 1179 and YPM 2594 to be referable to *P. occidentalis* and *P. ingens* respectively. Until evidence is brought forth that YPM 1179 and YPM 2594 pertain to species other than *P. occidentalis*

and *P. ingens*, I prefer to retain Eaton's (1910) specific designations for these skulls.

Conclusions

Whereas a considerable amount of work has been done toward elucidating the functional morphology of *Pteranodon* (Bramwell and Whitfield 1974, Stein 1975, 1976, Mateer 1975, Brower 1983, see also Padian 1980, 1983), the species-level taxonomy of *Pteranodon* and the closely related genus *Nyctosaurus* are in a state of disarray. In this paper I have clarified and commented on the type material of species of *Pteranodon* and *Nyctosaurus* housed in the Yale Peabody Museum. Such clarification is necessary before a thorough revision of all Pteranodontidae, encompassing specimens in numerous museums on several continents (see Wellnhofer 1978) can be carried out. Preliminary to such a revision, I make the following systematic suggestions: 1) *Nyctosaurus nanus* may be better referred to *Pteranodon*, as originally proposed by Marsh (1881), than to the genus *Nyctosaurus* (type species, *N. gracilis*). 2) *Pteranodon longiceps* and *P. marshi* are both junior subjective synonyms of *P. ingens*. 3) *P. comptus* is a junior subjective synonym of *P. velox*. 4) *P. eatoni* is a junior subjective synonym of *P. occidentalis*.

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